Variability in the Repertoires and Singing Behavior of Male and Female ‘I‘iwi (*Drepanis coccinea*)

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Abstract

Oscine passerines (songbirds) are notable for their complex, learned songs and an immense variability of vocal characteristics across the clade. Studying oscine vocal behavior can teach us about the selection forces that drive songbird evolution, but more research is needed on many species, especially with regard to female singing in tropical, monomorphic species. In this study, I cataloged and described the vocalizations and vocal behaviors of ‘i‘iwi (*Drepanis coccinea*), a Hawaiian honeycreeper, and compared male and female repertoire size, repertoire content, and vocalization rate. I recorded the vocalizations and behavior of individual ‘i‘iwi at Hakalau Forest National Wildlife Refuge, then examined spectrograms of ‘i‘iwi vocalizations, classified syllable types, and recorded quantitative measurements of time and frequency for each syllable. I selected seven male and six female ‘i‘iwi for statistical analysis. I observed whisper song, duetting, female solo singing, and females vocalizing from the nest among other behaviors, and was able to characterize a few common modes of ‘i‘iwi vocal behavior. I found no significant difference between male and female ‘i‘iwi in repertoire size, rate of vocalization, or proportion of shared syllables. A network analysis for modularity found that ‘i‘iwi repertoires are significantly modular, but modules mostly comprised single individuals rather than grouping ‘i‘iwi by sex. Additional measurements showed that ‘i‘iwi repertoires were highly individualistic. Overall, this study reveals previously unknown details about ‘i‘iwi vocal behavior and provides a baseline of knowledge that will contribute to ‘i‘iwi population monitoring tools and provide insight into the evolution of behavioral traits in ‘i‘iwi, among Hawaiian forest birds, and among songbirds worldwide.
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Introduction

Vocal signaling is an important communication tool for many animal taxa. Most animals develop these signals innately, i.e., without environmental input; however, in a few taxa, complex species-specific signals must be learned (Beecher & Brenowitz 2005). The oscine passerines, or “songbirds,” are a sub-order of birds partly defined by the highly developed vocal systems of the members of this group, and particularly their learned vocalizations. There is immense diversity among songbirds in repertoire size, repertoire variability within a population or species, vocalization function, and learning plasticity. This variability may be driven by selective pressures such as sexual selection for large repertoires, or an increase in reproductive success among birds that share songs with their neighbors (Beecher & Brenowitz 2005). Some studies suggest that some aspects of variation between species may be driven by phylogenetic history (Price & Lanyon 2004) or ecological conditions such as climate and species mobility (Handley & Nelson 2005). Studying songbird vocalizations can provide insights into the complex relationships between oscine vocal behavior, ecological conditions, and oscine evolution.

Traditionally, songbird vocalizations are classified as calls or songs based on a combination of structural and behavioral characteristics. The smallest unit or element of vocalization is a short, continuous signal called a note, and a collection of notes is called a syllable, with songs usually comprising multiple syllables (Konishi 1985, Bonnevie & Craig 2018). Calls are generally very simple, often one-note vocalizations used by both sexes and birds of all ages to convey a variety of information in different contexts, including announcing a food source, warning of a predator, or indicating aggression toward another bird (Marler & Slabbekoorn 2004, Kroodsma 2005). Songs are, very generally, longer and more complex
polysyllabic vocalizations typically used to defend territory or attract mates, and in oscines are typically learned from parents or neighbors rather than inborn (Spector 1994, Marler & Slabbekoorn 2004, Kroodsma 2005). However, due to high variation among species in the function and seasonality of song, Bonnevie and Craig (2018) have suggested a strictly structural definition that is more widely applicable. By their definition, a song is “a sequence of several vocal elements with species-specific characteristics, performed with a particular rhythmic pattern, which serves for intraspecific communication in birds” regardless of function, with song elements separated by silent intervals of 1 s or less, and intervals of < 10 s between songs in a song bout.

Variations in oscine singing behavior—repertoire size and song sharing

There are a finite number of songs or song types that an individual bird can learn and remember—this is a bird’s repertoire. Repertoire size is highly variable among oscine species. About 30% of songbird species have single-song repertoires, and about another 50% have small repertoires of five or fewer song types; other species have moderate repertoires of about ten (e.g. song sparrow, *Melospiza melodia*), large repertoires of more than 100 (e.g. western marsh wren, *Cistothorus palustris*), or even very large repertoires of more than 1000 (e.g. brown thrasher, *Toxostoma rufum*) (Beecher & Brenowitz 2005).

There is strong evidence that repertoire size in some songbirds with large repertoires is driven by female sexual selection (Searcy & Andersson 1986, Catchpole & Slater 2008, Searcy & Yasukawa 1996, Gil & Gahr 2002, Forstmeier & Leisler 2004). However, since the majority of songbirds have small or single-song repertoires, there must be other selective pressures at work. It is possible that there are high costs associated with large repertoires, such as a demand
for more brain space (Garamszegi & Eens 2004) or the developmental and energetic costs required to support a complex network of brain nuclei devoted to song learning (Nowicki et al. 1998).

Selection for song sharing may contribute to smaller repertoires. Song sharing is when territorial neighbors or members of a group share more songs with each other than with outsiders or newcomers. A variety of studies have suggested that song sharing can contribute to success in acquiring and holding territory (Beecher et al. 1997, Brown & Farabaugh 1997, Payne & Payne 1997, Beecher et al. 2000, Wilson et al. 2000, Lachlan et al. 2004) or can indicate male fighting ability to females (Vehrencamp 2000), therefore increasing reproductive success. In a phylogenetic study of 65 populations in the family Fringillidae (finches), Handley and Nelson (2005) found that song sharing was responsive to species’ mobility and breeding latitude; a species that was sedentary or had a low breeding latitude had higher song sharing than a species that was migratory or had a high breeding latitude. It is not necessary for a bird to have a large repertoire in order to share songs with a selected set of individuals; therefore in some species song sharing could have a negative effect on repertoire size, counteracting the positive effect of sexual selection for large repertoires (Beecher & Brenowitz 2005).

Songbirds are often described as being closed-ended or open-ended song learners, i.e., they are able to learn new songs only during a relatively short period of time and then their repertoire becomes fixed, or they continue to learn new songs throughout their life. Beecher & Brenowitz (2005) suggest that some open-ended learners may add and drop songs each year in order to maximize song sharing with new neighbors, as has been observed in great tits (Parus major) (McGregor & Krebs 1989), yellow-rumped caciques (Cacicus cela) (Trainer 1989), American redstarts (Setophaga ruticilla) (Lemon et al. 1994), scarlet rosettines (Carpodacus
erythrinus) (Martens & Kessler 2000), and common blackbirds (*Turdus merula*) (Rasmussen & Dabelsteen 2002). They argue that repertoire size should tend to be smaller for open-ended learners than for comparable closed-ended learners, which must start with the largest possible repertoire in order to increase the chances of matching with a new neighbor’s song. Indeed, most open-ended learners that replace songs in their repertoire have been found to have smaller repertoires than comparable closed-ended learners (McGregor & Krebs 1989, Lemon et al. 1994, Payne & Payne 1997, Griessmann & Naguib 2002, Kipper et al. 2004). Several experiments comparing closely related species or subspecies with different repertoire sizes found that the differences in repertoire size were driven by genetically-based differences in the song-learning programs of those taxa (Kroodsma & Canady 1985, Marler & Peters 1988).

**Individual variability**

Variation exists among the repertoires and vocal characteristics of individuals within a species. This variation may allow animals to identify specific individuals by their vocalizations, and could eventually be used by researchers for identification and monitoring of individuals (Terry et al. 2005, Laiolo et al. 2007, Mennill 2011). Songbirds may vary individually in their repertoire of songs, song types, or syllables (Thompson 1970, Cicero & Benowitz-Fredericks 2000, Petrusková et al. 2016), or in the use of subunits of song as individual signatures located in specific phrases or syllables (Nelson & Poesel 2007, Wegryzyn et al. 2009, Osiejuk 2014). They may also vary individually in the order of song elements (Briefer et al. 2014), in the proportion of song units (Sandoval et al. 2014), or in voice characteristics independent of syllable content or song type, such as song duration or minimum, maximum, and peak frequencies (Weary et al. 1990, Weary & Krebs 1992).
Sex and singing

The relationship between sex and singing behavior varies widely across the oscines. In northern temperate regions, where historically most bird song research has been done, male song is more abundant and evident than female song (Morton 1996, Slater & Mann 2004, Catchpole & Slater 2008, Fjeldså 2013). For this reason, it was once believed that males do all of the singing in the majority of oscine species (Collins 2004, Kroodsma 2005). However, the majority of bird species exist in the tropics, and female singing has been found to be common there (Odom & Benedict 2018), as well as in the subtropics, southern hemisphere temperate zones, and arid zones of Australia and Africa (Robinson 1948, Hartshorne 1958, Slater & Mann 2004). Females have also been found to sing in many temperate-breeding species (Benedict 2008, Najar & Benedict 2015, Krieg & Getty 2016). Female singing has been found in 42% of passerine species in the United States and Canada and in 43% of oscine songbirds in Europe (Benedict 2008, Garamszegi et al. 2007, Rodewald 2017). No songbird species where only females sing has been described (Webb et al. 2016).

The higher occurrence of female singing in the tropics, subtropics, and southern temperate zones may be related to, among other factors, low mortality rates (resulting from a milder climate), abundant resources, and the absence of a need to migrate, which in turn may result in stronger pair-bonding and territoriality (Yom-Tov et al. 1994, Slater & Mann 2004). In the arid zones of Australia and Africa, the irregularity of the climate may require birds to breed whenever conditions are favorable, and vocalizations from both sexes may assist in bringing the birds into breeding condition (Robinson 1948).
The presence of female singing has also been found to be strongly associated with more elaborate female coloration and reduced sexual dichromatism in a species; Webb et al. (2016) suggest that it is likely that the two traits have overlapping, reinforcing functions and do more to accurately convey the condition or status of the signaling individual than either trait on its own.

There is evidence that female singing is a basal trait that occurred among the early ancestors of all songbirds (Odom et al. 2014), suggesting that research is needed to investigate the selection pressures that caused females to stop singing in some species while maintaining song in both sexes in other species (Price 2015).

Sex-specific information about song exists for only 27% of oscine species; of that set, female singing is present in 64% of species (Webb et al. 2016). The species that lack sex-specific song information are often monomorphic, tropical species in poorly studied or difficult-to-access regions (Price et al. 2009, Odom et al. 2014, Webb et al. 2016). Due to the known prevalence of female singing in general and especially in the tropics and among monomorphic species, it is likely that female singing is present in a high proportion of these under-studied species (Odom & Benedict 2018).

Female song has a variety of possible functions. Although female territories, unlike male territories, may not be obtained for the specific purpose of attracting a mate, females may have as strong a reason as males to defend their territories from intruders that might compete for food, attempt to take over nest sites, or engage in extra-pair copulations with her mate (Collins 2004). Females in a variety of species are known to sing to defend territories, including European robins (Erithacus rubecula) (Lack 1965), superb fairy-wrens (Malurus cyaneus) (Cooney & Cockburn 1995), orange-billed sparrows (Arremon aurantiicostris) (Hart et al. 2013), and Australian magpies (Gymnorhina tibicen) (Brown & Farabaugh 1991). In other species, female song may
be used in mate attraction (Langmore et al. 1996a), mate defense (Yasukawa & Searcy 1982), breeding synchronization (Sonnenschein & Reyer 1983, Gahr & Güttinger 1986), or maintaining the pair bond (Gahr & Güttinger 1986). Females may also use song attract a male for extra-pair copulation or to induce copulation with a mate (Collins 2004).

A specific form of singing behavior known to occur in the females of certain species is duetting. Duetting occurs when members of a mated pair sing together in combination, either synchronous or alternating with their partner (Langmore 1998). This behavior has been studied in greater detail than female solo singing (Slater & Mann 2004). Duetting has been described in over 200 species of birds, and is estimated to occur in 3-4% of passerine species worldwide (Hall 2004). Duetting behavior has a strong association with tropical species and may also be associated with long-term monogamy, year-round territoriality, and sexual monomorphism (Thorpe et al. 1972, Farabaugh 1982, Malacarne et al. 1991, Catchpole & Slater 2008). The duet may function in territorial defense, and may in fact be more effective than solitary defense (Collins 2004). In duetting dusky antbirds (Cercomacra tyrannina; a sub-oscine passerine) (Morton 1996) and Polynesian megapodes (Megapodius pritchardii; a galliform) (Goth et al. 1999), each member of the pair may be able to defend their territory against same-sex intruders. In bay wrens (Cantorchilus nigricapillus), the duet may be used by both members of the pair for mate guarding, but with male and female song having different roles; female song in the duet repels female intruders, while the function of the male’s song is to guard his mate from extra-pair copulations (Levin 1996a, b).
Sexual dimorphism versus monomorphism

The degree of sexual dimorphism or monomorphism in various species may be linked to variability in other aspects of vocal behavior, besides the presence or absence of female song. However, clear patterns in this relationship are difficult to determine. Hartshorne (1958) states that monomorphism is correlated with a high degree of “musical development,” i.e., variety, purity of tone, frequency range, and carrying power. Shutler and Weatherhead (1990) found a positive correlation between the degree of dichromatism and time spent singing among wood warblers. On the other hand, Ornelas et al. (2009) found no relationship between dichromatism and song complexity among trogons, and Mason et al. (2014) found no relationship in the degree of plumage elaboration and the complexity of song among the males of 301 tanager species. In a phylogenetic study of New World blackbirds, Price and Lanyon (2004) did find that the relative degree of sexual size dimorphism correlated with changes in song organization and structure, although different aspects of song were affected in different lineages. Conflicting results may reflect biological and evolutionary differences among taxa, as well as methodological differences among different studies (Webb et al. 2016). Price and Lanyon (2004) treat sexual dimorphism as a measure of sexual selection, and point out that song presents a wide variety of targets for selection, resulting in different taxa responding to this selection in different ways.

‘I’iwi (Drepanis coccinea)

The ‘i’iwi (Drepanis coccinea) (Figure 1) is an oscine songbird in the family Fringillidae (true finches), subfamily Carduelinae, Hawaiian honeycreeper group, tribe Drepanidini (Raikow 1977, Sibley & Ahlquist 1982, James & Olson 1991, Tarr & Fleischer 1995, Groth 1998, Zuccon et al. 2012). It is a tropical species endemic to the Hawaiian Islands and is non-migratory,
although it is known to fly more than a dozen kilometers while foraging (Guillamet et al. 2017) and does not maintain a territory year-round (Fancy and Ralph 1998). ‘I’iwi appear to be monogamous within the breeding season but are not known to remain monogamous long-term (Fancy & Ralph 1998). ‘I’iwi are sexually monochromatic (Fancy & Ralph 1998) and exhibit a high degree of size monomorphism; males are 5-10% larger than females on average (Fancy et al. 1993), but there is a 75% rate of crossover in size between males and females (E. H. Paxton, personal comm.) Both males and females are known to sing (Fancy & Ralph 1998).

**Figure 1.** Adult ‘i’iwi (*Drepanis coccinea*).

The ‘i’iwi’s vocalizations and vocal behavior have not previously been studied in detail. Wilson and Evans (1890) describe a “peculiar… very powerful… flute-like” call as *ta-weet, ta-
weet, ta-wee-ah, and a “somewhat sweet and plaintive song.” Perkins (1903) describes the song of the ‘i‘iwi as “harsh in the extreme” and “harsh, strained, and discordant… cracked… [as if] forced out with difficulty,” and describes a couple of calls as “a rather loud unmusical squeak” and “a clear and distinct whistle.” Munro (1944) describes ‘i‘iwi song as like “the creaking of a wheelbarrow but a little more musical.” Eddinger (1970) describes a call used to establish contact between birds traveling together or by the male to call the female from the nest for courtship feeding, “harsh and metallic… loud squeak,” eek or coo-eek. He describes the same “distinct whistle” as Perkins (1903) and observed it most often used as an alarm call. Eddinger describes an ‘i‘iwi song as “squeaky ‘like a rusty hinge,’” a “short and harsh” ii-wi or ee-vee, rising in inflection. Eddinger also describes a vocalization from female ‘i‘iwi during courtship feeding solicitation as similar to the food calls of begging fledglings. He did not observe females singing or calling from the nest.

‘I‘iwi sing throughout the year, but on Hawai‘i Island sing more persistently from October through December, the beginning of ‘i‘iwi breeding season on that island (Ralph & Fancy 1994). Calls and songs are somewhat variable from between different locations (Perkins 1903). ‘I‘iwi males sing from selected perches, usually live or dead branches of ‘ōhi‘a lehua (Metrosideros polymorpha) trees and will occasionally sing while in flight, but do not have a specific flight song (Eddinger 1970).

Research objectives

The ‘i‘iwi is an ideal subject of study to shed light on the effects of evolutionary history, climate, mobility, female singing, and monomorphism on the evolution of singing behavior in the oscine clade. However, we currently lack a detailed record of ‘i‘iwi vocalization types, as
well as information on the size of an individual repertoire, amount of vocal variability between individuals, the degree of song sharing among neighbors, details of song structure and complexity, details of vocalization rate and vocal range, and the extent to which vocalizations and vocal behavior differ between the sexes. My objective is to catalog and describe ‘i‘iwi vocalizations and vocal behaviors and to compare male and female repertoire size, repertoire content, and vocalization rate.

**Hypotheses**

**Repertoire size**

**H1₀**: There is no difference in individual repertoire size between male and female ‘i‘iwi.

**H1₁**: There is a difference in individual repertoire size between male and female ‘i‘iwi, reflecting differing sex roles in territorial defense and mate attraction.

**Vocalization rate**

**H2₀**: There is no difference in vocalization rate between male and female ‘i‘iwi.

**H2₁**: There is a difference in vocalization rate between male and female ‘i‘iwi, reflecting differing sex roles in territorial defense and mate attraction.

**Repertoire relatedness**

**H3₀**: There is no difference in repertoire content between male and female ‘i‘iwi.

**H3₁**: Repertoire content is more similar within each sex than between sexes, reflecting differing sex roles in territorial defense and mate attraction.
Methods

Study species

The ‘i‘iwi is a nectarivorous Hawaiian honeycreeper with a current home range that encompasses parts of the islands of Hawai‘i, Maui, Moloka‘i, O‘ahu, and Kaua‘i (Fancy & Ralph 1998). ‘I‘iwi are approximately 15 cm long and 16-20 g (Fancy & Ralph 1998). Adults are bright vermilion with black wings and tail and a small patch of white on the inner secondaries of the wing; in juveniles the body feathers are a dull yellow with black speckling.

The most distinctive feature of the ‘i‘iwi is its long (25-28 mm; Fancy & Ralph 1998), deeply decurved, salmon-orange bill. The ‘i‘iwi’s bill is a famous example of probable coevolution with the curved, tube-shaped corollas of endemic lobelioids (Campanulaceae), which historical accounts indicate were the preferred food source of ‘i‘iwi (reviewed by Smith et al. 1995), and probably also the similarly-shaped endemic Stenogyne mints (Lamiaceae) and Hibiscadelphus (Malvaceae). The primary nectar source for ‘i‘iwi currently is the abundant ‘ōhi‘a lehua, although they take nectar from a wide variety of species, including the endemic māmane (Sophora chrysophylla), ‘ākala (Rubus hawaiiensis), and ‘ōhelo (Vaccinium spp.), and the non-native banana poka (Passiflora mollissima) and Japanese honeysuckle (Lonicera japonica). Arthropods also make up a significant portion of their diet (Fancy & Ralph 1998).

Study area

Data collection and field observations were conducted within the Hakalau Forest National Wildlife Refuge on the island of Hawai‘i at two banding sites, Pua ‘Ākala (PUAK; 19°47.24’N, -155°19.46’W) and Pedro (PEDR; 19°49.62’N, -155°17.96’W). Both sites may be characterized as a transitional zone between old-growth ‘ōhi‘a-dominated rainforest and an
ōhi’a and alien grass-dominated savannah environment altered by historic cattle grazing. Pua ʿĀkala and Pedro are located about 5 km apart, at approximately 1890 m and 1630 m above sea level, respectively. During the non-breeding season, Guillaumet et al. (2017) have documented ʻiʻiwi traveling on average 12.74 ± 0.39 km and as far away as 19.64 km from their breeding sites, and during the breeding season individuals sometimes leave their territories for foraging flights of likely up to several kilometers (Baldwin 1953, Ralph & Fancy 1995); therefore, ʻiʻiwi recorded at the two sites were considered to be part of the same population.

The sites were chosen due to a high abundance of ʻiʻiwi that had been banded by the Hawaiʻi Forest Bird Demography Project (HFBDP). ʻIʻiwi were captured using mist nets and sexed via breeding condition—the presence of a large or medium cloacal protrusion (CP) in breeding males or a brood patch (BP) in breeding females—or quantitative methods—length of culmen and wing chord determining the probability that an ʻiʻiwi is male or female, with males generally larger than females. Birds were then uniquely banded with a US Fish and Wildlife Service numbered aluminum leg-band and three additional colored plastic bands and released.

**Acoustic recording and processing**

Recordings and observations were made during ʻiʻiwi peak breeding season in two consecutive years, from February 21 to June 13, 2015, and from April 26 to May 24, 2016, with the majority of the data collected in the 2015 breeding season. Recordings were made of color-banded ʻiʻiwi and unbanded ʻiʻiwi attending active nests. Color-banded ʻiʻiwi were re-sighted with binoculars, with re-sighting efforts concentrated in an area within approximately 200 m of the mist nets, where re-sights of banded birds were most frequent. Band combinations of re-sighted birds were recorded and later matched with sex in the HFBDP database. Active ʻiʻiwi
nests were located by A. T. Beck or HFBDP field crews. Only female ‘i‘iwi are known to sit on nests during both the incubation and nestling stages (Eddinger 1970), so sex of unbanded birds was determined by their behavior at the nest (females by nest sitting, males by interacting with their mate, e.g. provisioning her).

Focal ‘i‘iwi were identified by either re-sighting or nest monitoring and their vocalizations were recorded using a Sennheiser shotgun microphone with a Rycote Softie sleeve and a Marantz PMD661 Digital Recorder. The following data were recorded during observations: start time, bird ID (color combo or nest number and sex), vocalization category (silent or vocalizing), activity category (perched, foraging, flying, preening, at or near nest), social category (solitary, aggressive, interacting with mate, interacting with parent or fledgling, other), any other potentially relevant details, observation end time, location (UTM), and Marantz recording number (if applicable). These observational notes were made verbally and recorded on a Sony IC voice recorder. Throughout the observation, changes in any category were noted as they occurred.

All sound files were analyzed using Raven Pro 1.5 interactive sound analysis software (Cornell Lab of Ornithology, New York). A selection table was created for each recording, associating each selected syllable with start time, end time, delta time, minimum frequency, maximum frequency, peak frequency, syllable ID, and bird behavior categories.

**Repertoire classification/composition**

‘I‘iwi vocalizations were described and classified by an analysis of their structure on a spectrogram with frequency in kHz on the y-axis, time in seconds on the x-axis, and signal power indicated by its color or shade. The smallest unit of a vocalization was classified as a
note, a signal or set of signals that were continuous on the time axis. A syllable was classified as a group of notes in a set pattern never found separately from each other. Vocalizations were classified by syllable, with each unique syllable assigned a unique alphanumeric moniker based on the number of notes.

Using the classification of the syllables, I was able to identify notable features and a few common modes or types of ‘i‘iwi singing behavior, which can be described in terms of songs and song bouts. Adapting the song and song bout definitions suggested by Bonnevie and Craig (2018), a song was classified as a set of one or more song syllables, separated by intervals of no more than 1 s in duration (Figure 2) and a song bout was a set of one or more songs, separated by intervals of < 10 s.

**Figure 2.** From Konishi (1985), time-frequency sound spectrogram of a white-crowned sparrow (*Zonotrichia leucophrys*) song, illustrating song components. Groupings of syllables called phrases and phrase types such as whistles, trills, and buzzes were not used in my analysis.
Assessing statistical power

For statistical comparisons between individual repertoires to be meaningful, I needed to have confidence that I had captured most of an individual ‘i’iwi’s repertoire. I selected seven males and six females for which I had the largest cumulative amounts of recorded and analyzed observation time. For each individual I produced accumulation curves showing the rate of accumulation of new unique syllables over time (Figure 3, Figure 4). Females had reached an asymptote within 1200 s of observation, and the majority of males had reached an asymptote after 1000 s of observation, so I determined that I could be reasonably confident of having captured most of these individuals’ repertoires, and therefore would be able to make statistical comparisons (Table 1).
Figure 3. Accumulation of unique syllables types with cumulative observation time of seven male ‘i’iwi: DO:KX (gray), DW:DX (red), KR:OX (green), KX:DG (blue), OO:WX (orange), WX:DY (purple), and YW:WX (black).
Figure 4. Accumulation of unique syllables types with cumulative observation time of six female ‘i’iwi: DY:OX (black), WX:RD (gray), YG:PX (blue), N16F (green), N17F (orange), and N18F (purple.).
Table 1. Observation details of the 13 ‘i‘iwi used in statistical analyses. From left to right: number of vocalizations, mean vocalizations per minute, number of syllable types, number of syllable types observed more than once, total observation time in seconds, number of recordings, number of recording days, observation date range, site, and how sexed. Individuals are identified by their unique color-band combination and/or by nest number. For ‘i‘iwi that were captured and sexed multiple times, “How sexed” indicates the most definitive method used. *WX:RD has a confusing capture history; WX:RD was sexed female by quantitative methods on first capture, recorded as unknown sex on second capture, and sexed female by quantitative methods but with a small CP on third capture (recording a small CP is not considered a definitive male identification).

<table>
<thead>
<tr>
<th>Males</th>
<th># Voc.</th>
<th>Mean voc./min</th>
<th># Syl. Types</th>
<th># Syl. Types MTO</th>
<th>Tot. Obs. Time (s)</th>
<th># Rec.</th>
<th># Rec. Days</th>
<th>Obs. Date Range</th>
<th>Site</th>
<th>How sexed</th>
</tr>
</thead>
<tbody>
<tr>
<td>DO:KX</td>
<td>772</td>
<td>11.2</td>
<td>68</td>
<td>53</td>
<td>3546.5</td>
<td>6</td>
<td>2</td>
<td>02/23/15–03/29/15</td>
<td>PUAK</td>
<td>CP, large</td>
</tr>
<tr>
<td>DW:DX</td>
<td>80</td>
<td>2.2</td>
<td>20</td>
<td>16</td>
<td>1613.5</td>
<td>7</td>
<td>1</td>
<td>03/08/15</td>
<td>PUAK</td>
<td>CP, medium</td>
</tr>
<tr>
<td>KR:OX</td>
<td>124</td>
<td>2.6</td>
<td>30</td>
<td>25</td>
<td>1831.5</td>
<td>8</td>
<td>2</td>
<td>04/06/15–05/02/15</td>
<td>PUAK</td>
<td>CP, large</td>
</tr>
<tr>
<td>KX:DG</td>
<td>77</td>
<td>2.4</td>
<td>13</td>
<td>11</td>
<td>2999.5</td>
<td>9</td>
<td>4</td>
<td>05/29/15–06/12/15; 04/26/16</td>
<td>PEDR</td>
<td>CP, large</td>
</tr>
<tr>
<td>OO:WX</td>
<td>67</td>
<td>5</td>
<td>19</td>
<td>14</td>
<td>1203.5</td>
<td>1</td>
<td>1</td>
<td>03/22/15</td>
<td>PUAK</td>
<td>CP, medium</td>
</tr>
<tr>
<td>WX:DY</td>
<td>17</td>
<td>0.8</td>
<td>10</td>
<td>4</td>
<td>1054.5</td>
<td>4</td>
<td>2</td>
<td>05/21/15–06/12/15</td>
<td>PEDR</td>
<td>CP, medium</td>
</tr>
<tr>
<td>YW:WX</td>
<td>133</td>
<td>4</td>
<td>23</td>
<td>20</td>
<td>2144</td>
<td>16</td>
<td>3</td>
<td>02/21/15–03/15/15</td>
<td>PUAK</td>
<td>CP, large</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Females</th>
<th># Voc.</th>
<th>Mean voc./min</th>
<th># Syl. Types</th>
<th># Syl. Types MTO</th>
<th>Tot. Obs. Time (s)</th>
<th># Rec.</th>
<th># Rec. Days</th>
<th>Obs. Date Range</th>
<th>Site</th>
<th>How sexed</th>
</tr>
</thead>
<tbody>
<tr>
<td>DY:OX (N13F)</td>
<td>7</td>
<td>0.2</td>
<td>6</td>
<td>2</td>
<td>1788.5</td>
<td>6</td>
<td>2</td>
<td>03/14/15–03/29/15</td>
<td>PUAK</td>
<td>Quant.; nest-sitting; BP, molting</td>
</tr>
<tr>
<td>WX:RD</td>
<td>537</td>
<td>19.4</td>
<td>47</td>
<td>40</td>
<td>2013</td>
<td>9</td>
<td>4</td>
<td>02/22/15–03/29/15</td>
<td>PUAK</td>
<td>Quant.*</td>
</tr>
<tr>
<td>YG:PX</td>
<td>370</td>
<td>15.5</td>
<td>14</td>
<td>7</td>
<td>1589</td>
<td>6</td>
<td>3</td>
<td>05/15/15–05/29/15</td>
<td>PEDR</td>
<td>BP, vascularized</td>
</tr>
<tr>
<td>N16F</td>
<td>23</td>
<td>1.9</td>
<td>4</td>
<td>4</td>
<td>1499.5</td>
<td>1</td>
<td>1</td>
<td>03/29/15</td>
<td>PUAK</td>
<td>Nest-sitting</td>
</tr>
<tr>
<td>N17F</td>
<td>426</td>
<td>17.6</td>
<td>2</td>
<td>2</td>
<td>1254</td>
<td>1</td>
<td>1</td>
<td>05/15/15</td>
<td>PEDR</td>
<td>Nest-sitting</td>
</tr>
<tr>
<td>N18F</td>
<td>83</td>
<td>0.7</td>
<td>12</td>
<td>7</td>
<td>1677</td>
<td>1</td>
<td>1</td>
<td>05/15/15</td>
<td>PEDR</td>
<td>Nest-sitting</td>
</tr>
</tbody>
</table>
To assess my statistical power with this small sample size, I used the Species Accumulation Curve function in package “vegan” in R to plot the average accumulation rate of new unique syllables with the addition of new individuals, using 100 randomized permutations. I generated plots for the set of all unique syllables (Figure 5) and for the set of unique syllables observed more than once (to reduce statistical noise) (Figure 6); neither curve shows flattening, indicating high variability from individual to individual and low statistical power for comparing between individuals with this sample size.

**Figure 5.** Average accumulation rate of new unique syllables with the addition of new individuals, using 100 randomized permutations.
Figure 6. Average accumulation rate of new unique syllables with the addition of new individuals (including only syllables observed more than once), using 100 randomized permutations.

**Repertoire size**

I examined the distribution of individual repertoire sizes (using only syllables that were observed more than once) and found that the data were not normally distributed. I used the Wilcoxon rank sum test to compare the median repertoire sizes of male and female ‘i‘iwi, and found the coefficient of variation for male and female repertoires.

**Rate of vocalization**

To find the average rate of vocalization (syllables/min) for each individual, I compiled a list of recordings for each bird that contained at least 1.5 mins of a continuous observation
record. I divided the recordings into 1.5 min sections and used a random number generator to select 10 sections for each individual. I counted the number of syllables in 1 min of the section, leaving a 15 s unsampled buffer before and after the sample minute. I took the average of 10 sample counts to find the mean syllables/min for each individual. I found that the mean vocalization rates were not normally distributed. I used the Wilcoxon rank sum test to compare the median mean vocalization rates of male and female ‘i‘iwi, and found the coefficient of variation for male and female vocalization rates.

**Repertoire relatedness**

I used network analysis to examine the structure of relatedness among individual repertoires. In a network representation of ‘i‘iwi repertoires, syllables and individual birds are nodes that are linked to each other if a syllable occurs in an individual’s repertoire. For this study, I examined the network using a quantitative measure of modularity. A network is considered modular if it is composed of subgroups of closely adhering nodes. In this case, a modular network would show that certain sets of syllables are strongly associated with certain individuals or groups of individuals and not others. A quantitative measure of modularity not only shows whether or not an interaction between nodes occurs (i.e., the presence or absence of a syllable in individuals’ repertoires), but indicates the intensity of the interaction (i.e., how frequently or infrequently the syllable occurs in a repertoire).

The quantitative modularity metric $Q$ was calculated using the algorithm QuanBiMo (Dormann & Strauß 2013), which uses the hierarchical random graph approach described by Clauset et al. (2008). I used the `Bipartite` package in R to calculate $Q$. The value of $Q$ varies from 0 to 1, where a large value indicates a network with a large number of modules and/or
modules with a high degree of isolation (see Oleson et al. 2007 for details). To determine if the repertoires were significantly modular, 100 random networks were generated using the Vazquez null model (Vazquez et al. 2007), which fixes the probability of syllable detection for each node (i.e. individual or syllable). I calculated the modularity ($Q_0$) of the null models and evaluated whether $Q$ fell within the 95% confidence interval calculated from the null models. I standardized the modularity by finding the z-score of $Q$ ($ZQ$), calculated as:

$$ZQ = \frac{(Q - \overline{Q_0})}{SD_0}$$

where $\overline{Q_0}$ is the mean of all the $Q$ values of the null models and $SD_0$ is the standard deviation of the mean.

In addition to the network analysis, I explored the relatedness of individual repertoires in a number of other simple ways, considering only syllables that were observed more than once. I determined the percentage of syllables that are unique to a single individual, the percentage of syllables that are common in the repertoires of sampled ‘i’iwi, and the percentage of syllables common to only one sex (i.e., common among the members of one sex, and entirely absent among the members of the other). A syllable was considered “common” in a group if it was present in at least 50% of repertoires, and “very common” if it was present in approximately 90% of repertoires.

Finally, I determined what proportion of the syllables present in each individual’s repertoire is shared with at least one other bird, and what proportion is unique to that bird. I examined the distribution of the proportions of shared syllables in individual repertoires and
found that the data were not normally distributed. I used the Wilcoxon rank sum test to compare
the median proportions of shared syllables in male and female repertoires.

**Distribution of syllable use by individual**

Considering all observed syllables, I ranked the frequency of occurrence of syllables in
each repertoire and determined the most commonly observed syllables for each individual, i.e.,
the set of top-ranked syllables comprising more than 25% of that individual’s observed
vocalizations.

**Results**

**Repertoire classification/composition**

I identified 182 unique syllable types within the study group repertoires (see Appendix).
Of these, 119 syllable types were observed more than once.

Individual choice of syllables and songs during a song bout had an interactive element; it
was very common for multiple birds within earshot to use the same syllables and songs in the
same time period, sometimes overlapping with each other.

I observed and was able to roughly define a few common modes of vocal behavior. Five
of my focal males (DO:KX, DW:DX, KR:OX, OO:WX, and YW:WX) and one of my focal
females (WX:RD) engaged in what was clearly solo singing. Two common types of song bout I
observed I call structured singing and fast unstructured singing. Structured singing is
characterized by a bird perching in one place or periodically moving from perch to perch but
otherwise not engaging in any behaviors other than vocalizing, vocalizing at a fast rate or
building to a fast rate with a median interval between syllables of 0.617 s, and the presence of
some identifiable pattern or structure, such as repeated identical or nearly identical combinations of syllables; this was observed from males DO:KX, KR:OX, OO:WX, and YW:WX, and female WX:RD. Fast unstructured singing is also characterized by perching-only behavior and a similar vocalization rate (median interval 0.936 s), but no recognizable structure or pattern emerges during the song bout; this was observed from males DO:KX and DW:DX and female WX:RD. I also observed whisper song, which has not previously been described in the literature (cf. Eddinger 1970, Fancy and Ralph 1998). Whisper song is characterized by a lack of structure or pattern, a usually very fast vocalization rate (median interval 0.484 s), and generally much quieter vocalizations; birds may perch or multitask. I observed this behavior from males DO:KX, KR:OX, and KX:DG, and female WX:RD, as well as from two pairs of ‘i’iwi not in my study group which employed whisper song in duets (see paragraph on duetting below). Extended whisper song bouts were almost always observed before, during, or after a close interaction with the singer’s presumed mate, such as a provisioning bout.

Another commonly observed vocalization mode is slow unstructured vocalizing, which is characterized by a lack of structure or pattern, a slow vocalization rate (median interval 7.549 s), and multi-tasking behavior, i.e. birds punctuating other behaviors such as foraging with occasional vocalizations; the only study individual for which this behavior was not observed was female N17F. The final commonly observed vocalization mode is interact calling, which is characterized by a fairly high vocalization rate (median interval 1.170 s) and low syllable diversity, with bouts comprising long stretches of a single repeated one-note syllable type, or sometimes a few one-note syllable types, generally a raspy “squirk”-type sound. Interact calling is associated with female begging and mate provisioning; this behavior was observed from males KX:DG and OO:WX, and females YG:PX, N16F, N17F, and N18F.
Although the behavioral modes defined above occurred often enough to be recognizable and describable, it should be noted that vocalizing individuals did not always conform to these modes exactly, varying vocalization speed, structure, or other features of their behavior in ways that defy easy categorization.

Other modes of singing behavior were observed less frequently but contribute to a larger understanding of how ‘i‘iwi use song. ‘I‘iwi were sometimes observed to vocalize while flying, usually a single syllable uttered while crossing a short distance; on a couple of occasions, however, male OO:WX produced songs comprising multiple syllables uttered at a high vocalization rate.

Another notable ‘i‘iwi vocalization observed occasionally was duetting, in which pairs of individuals perched close together, both singing. I observed duetting amongst three pairs of birds, none of which were members of my study group. Duets comprised structured singing or whisper songs or both. Duets followed an alternating pattern, i.e. the individuals took turns rather than singing simultaneously, although sometimes there would be some overlap. How closely the songs and syllables of one singer matched its partner varied. Duets were frequently accompanied by wing fluttering by one or both individuals. Birds were sometimes observed preening or foraging during duetting bouts. In the first duet, the duetting pair and one or more nearby individuals (audible, but not visible) engaged in structured singing using the same or very similar songs and syllables. In the second duet, the duetting was preceded by an aggressive physical altercation with a third bird that afterward lingered in the area, producing similar structured songs to the duetting pair; the duetting pair also produced whisper song. In the third duet, duetting consisted entirely of whisper song and may have accompanied a mating event; no other birds appeared to be involved.
All four nesting female ‘i‘iwi in my study group (DY:OX, N16F, N17F, and N18F) were observed vocalizing from the nest, a behavior not previously described in the literature (cf. Eddinger 1970, Fancy & Ralph 1998). Females N16F and N18F were observed singing from the nest once each. N16F sang apparently in response to or in a duet with an unseen individual singing nearby, although the two birds produced different songs that did not share syllables. The unseen individual started with the same syllable every time, and when N16F sang it was always within 0.1-0.4 s of the first syllable of the unseen individual’s song; at least one other distant individual engaged in structured singing during this song bout, sharing a syllable with the nearby unseen individual.

**Repertoire size**

Of the set of syllables observed more than once, the median number of syllables in an ‘i‘iwi repertoire is 11. The median number of syllables among male repertoires is 16 (min = 4, max = 53, IQR = 10), and the median number of syllables among female repertoires is 5.5 (min = 2, max = 40, IQR = 4.5) (Figure 7). No significant difference between male and female repertoire sizes was found ($W = 8.5, p = 0.085$). The coefficient of variation (CV) among males is 82.5%, and the CV among females is 142.3%.
Figure 7. Median number of syllables in female and male repertoires, of the syllables observed more than once in the repertoires of the study group.

Rate of vocalization

The mean vocalizations per minute was calculated for each individual, then the median was found for all individuals, all males, and all females. The median mean vocalizations per minute for ‘i’iwi is 2.6. The median mean vocalizations per minute for males is 2.6 (min = 0.8, max = 11.2, IQR = 2.2), and the median mean vocalizations per minute for females is 8.7 (min = 0.2, max = 19.4, IQR = 16.075) (Figure 8). No significant difference between male and female
vocalization rates was found ($W = 22, p = 0.945$). The CV among males is 85.3%, and the CV among females is 99.5%.

![Figure 8. Median mean vocalization rate among females and males.](image)

**Comparing repertoire content and structure**

An analysis of the modularity of ‘i‘iwi repertoires compared to 100 null models found that ‘i‘iwi repertoires are significantly modular ($Q = 0.667, \bar{Q}_0 = 0.348, ZQ = 13.517, p < 0.01$).
The repertoires were grouped into 11 modules, most of them comprising a single individual, with the exception of a module formed by the individuals YG:PX, N16F, and WX:DY.

64% of syllables observed more than once are unique to a single individual; 36% are shared between two or more individuals. Of these shared syllables, there are no syllables common to at least 50% of individuals. Of syllables observed more than once that are unique to one sex or the other, there are no syllables common to at least 50% of individuals of that sex. However, 50% or more of the syllables in each individual repertoire are shared with at least one other individual (Figure 9). There is no significant difference in the median proportion of shared syllables between males and females ($W = 7, p = 0.052$).

**Figure 9.** Proportions (in percentages) of individual repertoires composed of syllables shared with at least one other individual and syllables unique to an individual, among syllables observed more than once.
The dominant or preferred syllables in an individual repertoire varied from individual to individual (Figure 11, a.-m.). For individual DO:KX, the most commonly observed syllables in the repertoire are 3B (9.20%), 1M (6.61%), 2F (6.35%), and 1B (4.92%). For DW:DX, the most commonly observed syllables are 3B (15%) and 1HH (12.5%). For KR:OX, the most commonly observed syllables are 1LL (19.35%) and 1NN (8.87%). For KX:DG, the most commonly observed syllables are 1A (22.08%) and 1CCCC (22.08%). For OO:WX, the most commonly observed syllables are 1FFF (22.39%) and 1A (16.42%). For WX:DY, the most commonly observed syllables are 1ZZ (23.53%) and 1FF (17.65%). For YW:WX, the most commonly observed syllables are 2A (15.79%) and 1C (12.78%). For DY:OX, the most commonly observed syllable is 1NNNNN (28.57%). For WX:RD, the most commonly observed syllable is 3A (32.02%). For YG:PX, the most commonly observed syllable is 1ZZ (84.05%). For N16F, the most commonly observed syllable is 1ZZ (52.17%). For N17F, the most commonly observed syllable is 1ZZZ (99.53%). For N18F, the most commonly observed syllable is 1FF (62.65%).
a) DO:KX

b) DW:DX
35
**Discussion**

**Repertoire classification/composition**

*Syllable classification*

In my analysis of ‘i’iwi vocalizations, I used the syllable as my basic unit of description, identifying 182 unique syllables. Although some recognizable patterns emerged in structured singing, i.e. certain ordered combinations of syllables that might be classified into recognizable song types, fast unstructured singing and slow unstructured singing were similarly prevalent behaviors in which songs were constructed of long strings of syllables in apparently near-random order or consisted of monosyllabic utterances with lengthy gaps between each vocalization. I found it prohibitively difficult to attempt to categorize ‘i’iwi vocalizations into unique,
recognizable, and comparable songs or song types, and chose instead to use the syllable as my basic unit.

Lynch (1996) argues that, from an evolutionary standpoint, the important unit of birdsong is the song meme, i.e., the unit of cultural transmission, or, “a song pattern that is transmitted from one bird to another during the learning process” (Lynch et al. 1989). In some songbird species, whole songs are transmitted (e.g., Slater et al. 1980, Beecher et al. 1994); in other species, individual syllables or blocks of linked syllables are copied and recombined with other syllables or blocks of syllables to make new songs (Marler & Peters 1982, Jenkins & Baker 1984). Depending on the species, then, a meme can be an individual syllable, a group of linked syllables, or a whole song. Individual syllables and occasionally groups of syllables appear to be the transmittable memes in ‘i‘iwi singing.

A few other Hawaiian oscines have been found to transmit memes at the sub-song level. Sebastian-Gonzalez and Hart (2017) classified memes at the syllable level for the Hawaiian honeycreeper ‘apapane (Himatione sanguinea) as well as ‘i‘iwi, and Fernandez (2018) found that syllables function as song memes for the Hawaiian thrush ‘ōma‘o (Myadestes obscurus).

‘I‘iwi vocalizations proved difficult to classify using the traditional, generalized definitions of calls and songs. On some occasions ‘i‘iwi would perch in an open area and produce polysyllabic vocalizations at a high rate with notable structure or pattern—clearly, territorial singing. On other occasions the same syllables would be observed with very different behavior: monosyllabic vocalizations, a low vocalization rate, a lack of structure or pattern, and interspersed with foraging or other behaviors. It is likely that the same syllable types function as both calls and units of song in different behavioral contexts. Since these syllables were observed
in a variety of behavioral contexts, I chose to define ‘i‘iwi song in the strictly structural sense suggested by Bonnevie and Craig (2018).

A clear example of flexibility in syllable use and function is the group of syllables associated with interact calling; different individuals of either sex used these same syllables in different ways. Syllable 1ZZ, which was used as a begging vocalization by females YG:PX and N16F, was used in fast singing bouts by male OO:WX and female WX:RD and in slow unstructured singing by males KX:DG and WX:DY. Syllable 1FF, which was used as a begging vocalization by female N18F, was used by males KR:OX, KX:DG, and WX:DY in slow unstructured vocalization, by male OO:WX in both slow unstructured vocalization and fast unstructured singing, and by male DO:KX in all common modes of vocalization. Syllable 1ZZZ, which was used as a begging vocalization by female N17F, appeared to be used as an aggression call by female YG:PX.

A lack of a clear dichotomy between songs and calls has been observed in other species, such as the alpine accentor. Female alpine accentors are variable in their use of a trill vocalization, some producing simple trill calls, others combining repeated trills with another syllable to produce simple song, and others combining trills with many different syllables to produce complex song (Langmore et al. 1996). It is possible that ‘i‘iwi use their vocalizations similarly. What I have described as slow unstructured vocalization may be a series of contact calls in that context; ‘i‘iwi may combine these call syllables in rapid, polysyllabic arrangements in order to create songs. In the absence of information on how the birds themselves understand and use these vocalizations, it is difficult to know precisely how to classify ‘i‘iwi vocalizations into songs or calls.
My results pertaining to the number of unique syllables recorded, which and how many of these syllables were observed more than once, and the extent to which syllables were shared among individuals may have been affected by my choice of methods in classifying unique syllables. I allowed for a certain amount of variation among individual vocalizations classified as the same syllable, particularly in regards to frequency range (kHz), the duration (seconds) of notes and gaps between notes, and the shape of notes as they visually appeared on the spectrogram. However, I was very conservative when it came to the number of notes or placement of notes within a syllable; any deviation from the pattern resulted in a separate classification.

A variety of approaches to meme classification exist in the literature. Some researchers allow for some variety in presence or absence of certain syllables or the number of notes comprising a syllable in the classification of songs (Figure 1, Beecher & Brenowitz 2005). Price (1998) and Price and Lanyon (2004) took a more conservative approach, classifying songs as the same song type only if songs were indistinguishable by visual inspection of spectrograms and by ear. Different classification methods may be appropriate for different species, depending on whether song learners imitate tutor songs, improvise from tutor songs, or invent new songs (Beecher & Brenowitz 2005). My conservative syllable classification would be most appropriate if ‘i‘iwi are song imitators; however, my approach may not accurately reflect how ‘i‘iwi learn, recognize, and use these syllables, or may classify as different syllables vocalizations that were merely cut short due to disruptions in the environment, and may have resulted in an artificially inflated number of syllable classifications.
**Song type matching**

I made a number of qualitative observations that provide insights into ‘i’iwi behavior in the larger context of the range of songbird behaviors. ‘I’iwi seem to frequently engage in song type matching, i.e., singing the same song type as another individual, when engaging in countersinging interactions with rivals. In cardinals, great tits, song sparrows, chaffinches, meadowlarks, European blackbirds, and some wrens, type matching appears to be a signal of aggression, whereas repertoire matching (singing a shared but not recently sung type) or singing an unshared song type were correlated with a lower probability of escalation of aggressive behavior (Hinde 1958, Lemon 1974, Kroodsma 1979, Krebs et al. 1981, Todt 1981, Falls 1984, McGregor et al. 1992, Beecher et al. 1996, Vehrencamp 2000); in several of these species, playback experiments have shown that birds react more strongly, i.e., approach the speaker, to a type-matching signal. In playback experiments, some species—western meadowlark, corn bunting, and wood thrush—avoid type-matching the playback song (Falls & Krebs 1975, McGregor 1986, Whitney 1991), whereas other species—cardinal, tufted titmouse, hill mynah, and banded wren—increase their tendency to type match (Lemon 1968, Bertram 1970, Schroeder & Wiley 1983, Vehrencamp 2000). It could be interesting to conduct interactive playback experiments with ‘i’iwi in order to determine what role type-matching plays in ‘i’iwi interactions and what level of aggression is signaled by matching song type with a rival.

**Whisper song**

On a number of occasions I observed whisper song, i.e. long, complex vocalizations produced at a lower amplitude than most other ‘i’iwi vocalizations, which have not previously been described in the literature regarding ‘i’iwi. Low-amplitude vocalizations have been
described in the literature of ~58% of North American bird species and ~21% of Neotropical bird species, but more information is needed on the prevalence, function, and structure of low-amplitude vocalizations in birds (Reichard & Welkin 2015). Among North American bird species for which we have information relating to function, low-amplitude songs, like high-amplitude songs, appear to have courtship and/or territorial functions, and in structure may be the same as or different from typical high-amplitude songs, depending on species (Reichard & Welkin 2015). As with high-amplitude songs, the majority of whisper songs are attributed to male birds (Reichard & Welkin 2015). ‘I‘iwi whisper song bouts did sometimes share a few syllables seen in typical high-amplitude singing, but the majority of the syllables were unique to the whisper songs, and a transition from high-amplitude song to whisper song always involved a change in the set of syllables used. ‘I‘iwi whisper songs were produced by both males and females and seem to be associated with courtship or strengthening of the pair bond, since extended whisper song bouts were almost always observed before, during, or after a close interaction with the singer’s presumed mate, such as a provisioning bout or mating. Some ‘i‘iwi whisper songs may have a territorial function, as one observation of whisper song occurred in a duet following an aggressive altercation with a rival bird and was produced alongside type-matched countersinging. Collecting more data on these specialized vocalizations could result in deeper understanding of ‘i‘iwi courtship and territorial behavior and contribute to a greater understanding of the function of and evolutionary forces driving the selection for this common but poorly understood behavior across many taxa.
**Duetting**

I observed both female solo singing and duetting. In many species, duets occur in the context of conflicts with neighbors, and may function in territorial defense or in guarding mates against same-sex rivals (Langmore 1998). The members of a duetting pair may have different functions for their songs; experiments suggest that the lead singer may sing to defend territory against a same-sex rival while the replying singer guards their mate by announcing their mated status, while the order in which the sexes sing varies by species (Langmore 1998). The duets I observed that involved high-amplitude song involved interactions with neighbors. One duet comprised a banded individual of unknown sex and an unbanded mate. The other duet comprised a banded male and an unbanded mate; at times it was hard to tell which bird was vocalizing, at other times it seemed more of a back-and-forth exchange than a lead song and a reply, but most of the time when a call-and-response pattern could be identified, the banded male seemed to be replying to the presumed female. The identity and sex of nearby rivals was unknown in both duets. More study on ‘i‘iwi duetting is needed to understand the structure, order, and function of duetting in this species.

**Singing from the nest**

Females N16F and N18F were observed singing from the nest. N16F apparently sang in reply to the song of a nearby individual. In an experiment with great reed warblers (*Acrocephalus arundinaceus*), approximately one-third of visits by unpaired females to a breeding female’s territory resulted in the mated female singing from the nest when the unpaired female was within hearing distance, suggesting a function in female-female competition for mates (Bensch & Hasselquist 1992). As the identity and sex of the lead singing ‘i‘iwi are
unknown in this encounter, it is unclear whether this was an occurrence of duetting with a mate, territorial defense against a same-sex rival, or if there was some other behavioral context.

**Male and female solo singing**

Only two males from the study group, KX:DG and WX:DY, were not observed singing. While the other five males were from the Pua ‘Ākala banding site, these two males were from Pedro and were recorded later in the season than the others. It is likely that a difference in their breeding status at the time of observation corresponds to the difference in their observed behavior.

My observations and descriptions of female solo singing in ‘i‘iwi are significant. Female solo singing has been somewhat neglected as a topic of study, and information on female solo singing is lacking for many species (Slater & Mann 2004). Only one female, WX:RD, was observed singing extensively, in both structured and fast unstructured modes. WX:RD greatly surpassed all other females in repertoire size and rate of vocalization. Indeed, she had the second-largest repertoire size of the entire study group, and the highest vocalization rate of the entire group.

An increase in female singing in species where female singing is rare may be a response to female-female competition, and is often more common or entirely limited to a short, specific period in the reproduction cycle (Langmore 1998). In song sparrows (*Melospiza melodia*), female song occurred in the period just before nest-building, mostly occurred during territorial conflicts between females with territories and female intruders, and was more common when population density was high, but never occurred in response to males attempting to settle within female territories (Arcese et al. 1988). In white-crowned sparrows (*Zonotrichia leucophrys*),
females sang in the pre-nest building period in years when snow-melt came late, resulting in increased competition for nesting sites; researchers were able to elicit female song via playback of male and female conspecific song in the pre-nest building period but not at other times (Baptista et al. 1993). Approximately one third of female great reed warblers (Acrocephalus arundinaceus) sang at intruders during the early nesting period (Kluyver 1955, Bensch & Hasselquist 1992), and one third of female starlings (Sturnus vulgaris) sang at intruders during the pre-laying and egg-laying periods (Sandell & Smith 1997). Yellow warblers (Dendroica petechia) were only observed to sing during aggressive interactions with female neighbors or by female intruders on their territories (Hobson & Sealy 1990). In the opportunistically polygynous species described above, female song may function in competition for territory or nesting sites, or in competition for mates (Langmore 1998). An experiment on female dunnocks (Prunella modularis) found that an increase in competition for male attention in the absence of competition for territories resulted in increased production of complex female songs, confirming a function of female song in competition for mates in this species (Langmore & Davies 1997).

Female singing to attract mates appears to be uncommon, and could not be confirmed in experiments on bay wrens, northern cardinals, or dunnocks (Levin 1996a, McElroy & Ritchison 1996, Langmore & Davies 1997). Mate attraction was found to be a function of female song among alpine accentors (Prunella collaris), a polygynandrous species with very large home ranges (Langmore et al. 1996b), and may be the function of a courtship song produced by male and female dusky antbirds (a sub-oscine passerine), a species with year-round territories (Morton 1996).

Females of a number of species have been shown to sing in order to coordinate breeding activities. Male and female slate-coloured boubous and black-headed grosbeaks (Pheucticus
melanocephalus) sing to coordinate nest relief, and female black-headed grosbeaks also sing to locate fledglings and maintain group cohesion (Sonnenschein & Reyer 1983, Ritchison 1983). Song is used by male and female northern cardinals to coordinate provisioning of young (Halkin 1997). The song of female red-winged blackbirds is used to encourage male nest defense (Yasukawa 1989).

WX:RD was one of two females in my study group that was not seen in association with an active nest. WX:RD may have been observed during a pre-nest building period when she may have been competing for territory with her female neighbors, which could explain her higher than average repertoire size and vocalization rate. Alternatively, she may have been observed post-nesting, and her singing may have been used to maintain communication with her fledgling or fledglings. WX:RD was observed interacting with other ‘i‘iwi on a few occasions. In one recording Feb. 22, 2015, WX:RD chased another ‘i‘iwi, and then a short time later an unbanded adult ‘i‘iwi came into close proximity with WX:RD for about a minute, during which time and for about 20 seconds after, WX:RD significantly increased her vocal rate and meme diversity. In a recording Feb. 23, 2015, WX:RD was observed in close interaction with male WK:YX and an unbanded ‘i‘iwi for almost four minutes, during which the three birds perched in the same tree close together, made soft vocalizations and preened. All three ‘i‘iwi had adult plumage. WX:RD and WK:YX were closer to each other than to the third bird. WK:YX was observed singing loudly a couple of times during this interaction, and the unbanded bird was observed with a stick in its mouth. In another recording on the same date, WX:RD and WK:YX interacted briefly, during which they were very close to each other in the same tree and WK:YX sang once. It is difficult to comprehend the context of these interactions without knowing the
identity of the unbanded birds and without a larger set of observations of WX:RD and WK:YX over a longer period.

It is also possible that WX:RD was misidentified as female. WX:RD was captured three times: on Nov. 14, 2014, identified as female by quantitative means, no cloacal protuberance (CP) or brood patch (BP); on Mar. 16, 2015, sex unknown, no CP or BP; and on May 7, 2015, identified as female by quantitative means, small CP, no BP. Because of WX:RD’s small size, it is statistically unlikely that WX:RD is male, but it is possible WX:RD is an unusually small male. A small CP could indicate male, but small CPs are often confused with normal, non-enlarged cloacal openings. In the absence of a brood patch, it is impossible to confirm with 100% certainty that WX:RD is a female. On the other hand, a female without a brood patch is not nesting, which, as discussed above, could also account for WX:RD’s unusual behavior. It should also be noted that WX:RD was observed interacting very closely—in a non-aggressive manner that I interpreted as courtship behavior—with WK:YX, a bird that has been identified as male both by quantitative means (Aug. 29, 2014) and by a medium CP (Apr. 29, 2015). This would also suggest that WX:RD is, in fact, female.

**Repertoire size**

The median individual repertoire size (syllables observed more than once) was 11, but there was high variability among individuals. DO:KX was an extreme outlier in the male group, with 53 syllables observed more than once, compared to the male median of 16. WX:RD was an extreme outlier in the female group, with 40 syllables observed more than once, compared to the female median of 5.5. The male median is higher than the female median, but high variability within the sample set resulted in no significant difference between the two groups. I cannot
reject the null hypothesis that there is no difference between individual repertoire size of male and female ‘i’iwi, but it is possible that a difference would be revealed with more or different data—using only ‘i’iwi recorded during the same time period or behavioral period (i.e., breeding vs. not breeding, or even different parts of the breeding period such as courtship, nest building, incubating, caring for nestlings, or caring for fledglings), collecting data for a longer swath of time for each individual so as to capture behavioral variability within individuals, or including more individuals in the study.

Individual repertoire size may have been artificially altered due to variable amounts of observation time per individual. Observation time for individuals in my study group ranged from 1054.5 s to 3546.5 s. I am fairly confident that the majority of each individual’s repertoire has been observed, as indicated by a flattening trend in they syllable accumulation curve for most individuals. Regardless of observation time, the number of new syllables added to an individual’s observed repertoire after the flattening of the curve would be less than the number of syllables added before the flattening trend, which would help to ameliorate any differences caused by observation time. However, the total observed repertoire size would be weighted to some extent by the observation time, which may have contributed to inaccuracies in the results.

Additionally, there is high variability from ‘i’iwi to ‘i’iwi in the number of recordings, the length of recordings, and the number of separate observation days represented in the recordings comprising the total observation time for each individual. My analysis treats each second of recording time as independent; in reality, vocalizations observed in the same recording on the same day are likely to be more similar than vocalizations observed in separate recordings days, weeks, or months apart. In this way, the temporal distribution of observation time for each individual may have an artificial effect on the observed repertoire size and content.
It is difficult to compare median ‘i‘iwi individual repertoire size or the range of individual repertoire size to other songbird species, since most of the literature on songbird repertoire size describes repertoire in terms of number of songs. If memes are comparable, whether syllables or songs, then ‘i‘iwi have moderate or large individual repertoires, larger than about 80% of songbird species (Beecher and Brenowitz 2005). ‘I‘iwi appear to construct songs nearly randomly from their available syllables, and I was unable to classify specific song types, although I did observe a few unique phrases (groups of syllables) or groups of similar phrases that occurred across multiple individuals. It is possible that with longer observation of more individuals, recognizable syllable patterns or songs would emerge.

Regardless, it is clear that observed syllable repertoire size of ‘i‘iwi is highly variable from individual to individual, or perhaps is highly variable for each individual depending on breeding status or other markers of behavioral change.

**Rate of vocalization**

The median mean vocalizations per minute was 2.6, but there was variability among individuals. DO:KX was an extreme outlier in the male group at 11.2 vocalizations per minute, compared to the male median of 2.6. The female group had a very uneven distribution, with three females in the 0.2-1.9 vocalizations per minute range, and three females in the 15.5-19.4 vocalizations per minute, both groups very far from the female median of 8.7. Female ‘i‘iwi either vocalized very little (below the median rate) or a lot (much higher than the group median). The female median is higher than the male median, but high variability with the sample set resulted in no significant difference between the two groups. I cannot reject the null hypothesis that there is no difference between individual vocalization rate of male and female ‘i‘iwi, but as
with my examination of repertoire size, it is possible that a difference would be revealed with more or different data.

Three of four female ‘i’iwi that were associated with active nests had very low vocalization rates, and the two females that did not have an observed association with an active nest had very high vocalization rates. It is possible that differences in vocalization rate among females may be linked to breeding status. It makes sense that females sitting on the nest would limit vocalizations to avoid attracting predators to the nest site, and indeed female ‘i’iwi vocalizing from the nest had not previously been described in the literature (Eddinger 1970, Fancy & Ralph 1998). However, this would make female N17F an outlier, as she was observed with a high rate of vocalization both on and off the nest, at a mean of 17.6 vocalizations per minute. The vast majority of N17F’s utterances were a begging-type vocalization, so perhaps she was being insufficiently provisioned by her mate.

It is also possible that male DO:KX’s much higher rate of vocalization compared to other males may also have been related to his breeding status. More detailed observation of male behavior would be required for a determination.

As with repertoire size, differing amounts and temporal distribution of observation time may have affected the observed mean vocalization rates. I attempted to account for this in my sampling methods; however, for individuals for which I had less recorded observation time or for which my observations covered a narrower total window of time, I may have captured a narrower sample of their full behavioral range, which may have artificially raised or lowered their observed mean vocalization rates.
Regardless, it is clear that observed vocalization rate of ‘i‘iwi is highly variable from individual to individual, or perhaps is highly variable for each individual depending on breeding status or other markers of behavioral change.

**Comparing repertoire content and structure**

**Network analysis**

In a quantitative analysis of the modularity of individual repertoire content, I found that ‘i‘iwi repertoires were significantly modular. However, 10 of the 11 modules comprised single individuals, suggesting that ‘i‘iwi repertoires are highly specialized to each individual, rather than shared to a certain degree with other individuals that share other behavioral or life history traits.

One module comprised three individuals, showing that syllables 1ZZ, 1CCC, 1WWW, 1PPPPP, 1SSSSS, and 1VVVVV were strongly associated with individuals YG:PX, N16F, and WX:DY. 1ZZ had a strong association with all three individuals. 1CCC had a strong association with YG:PX and WX:DY. 1WWW was only observed to be used by N16F, and was the second most common syllable in N16F’s repertoire after 1ZZ. 1PPPPP, 1SSSSS, and 1VVVVV were only observed to be used by YG:PX, and along with 1ZZ, 1CCC, and 1CCCC (not part of the module), were the most common syllables in YG:PX’s repertoire. On a few occasions individuals used the shared module syllables in the same vocalization bout, linking the syllables temporally and behaviorally. YG:PX used 1ZZ and 1CCC together on one occasion, 1PPPPP, 1SSSSS, and 1CCC together on another occasion, and potentially 1VVVVV and 1ZZ together on a third occasion (observation was brief, it is unclear if YG:PX grouped these together or was switching from one behavioral mode to another). WX:DY used 1CCC and 1ZZ together on one
occasion. On a number of other occasions, however, 1ZZ, 1WWW, and 1CCC were used by individuals (grouped within the module and not) without a temporal link to any of the other shared module syllables. There did not appear to be a relationship between the syllables and bird behavior.

YG:PX was a female at the Pedro site that was observed to be associated with a mate but not a nest. N16F was a female at Pua ʻĀkala with an active nest. WX:DY was a male at Pedro that was not observed to be associated with either a mate or a nest. The three individuals from the shared module did not share sex, location, or breeding status. It appears that the individuals were grouped together because of a strong association with one or two syllables (1ZZ and 1CCC), and the other syllables were grouped in the module because of a strong association with one of the grouped individuals. There is no clear behavioral or life history factor linking the three individuals together.

This analysis did not directly test whether or not there was a difference in repertoire content between male and female ‘i‘iwi. The network analysis did not create modules grouping individuals by sex, but rather indicated that each individual is unique in the content and preferred syllables of its repertoire.

*Proportion of unique/shared syllables*

Although most syllables in an individual’s repertoire are shared with other individuals, there are no syllables that are common to the majority of individuals. Shared syllables were observed to occur in the repertoires of 2-6 individuals. The majority of syllables observed appeared to be unique to a single individual. This corroborates the results of the network analysis, that ‘i‘iwi repertoires are highly individualistic in syllable content and frequency of
syllable use. The fact that many of the syllables in an individual’s repertoire are shared, but only
shared with a few birds, suggests that ‘i’iwi have a limited repertoire capacity, i.e., they cannot
learn and remember every single syllable they encounter. It is likely that ‘i’iwi engage in song
sharing, where they are more likely to share syllables with close neighbors than distant strangers,
and that it confers a territorial advantage to be able to match type-match when engaging in
countersinging with neighboring rivals. This could potentially be confirmed by collecting data
from a larger proportion of ‘i’iwi within a population and comparing repertoire content in the
context of territory location; neighboring birds would be expected to share more syllables with
each other than with more distant individuals.

It is also possible that more syllables were shared, or shared syllables were shared more
widely, than was observed. Different individuals used the same syllables at different frequencies
or as a different proportion of their repertoire. A syllable that was not observed to be used by a
specific individual may indeed have been in that bird’s repertoire, but may not be used frequently
enough by that bird to have been detected.

No sex-specific syllables were common to a majority of that sex. I was unable to reject
the null hypothesis that there is no difference in repertoire content between male and female
‘i’iwi. Again, ‘i’iwi repertoires seem to differ between each individual rather than grouping by
sex. Neither was there a difference between sexes in the proportion of an individual repertoire
comprising shared syllables versus unique syllables. Males and females do not appear to be
different in the degree to which their repertoires are shared or unique.
Individual preferred syllables

Each individual had a different set of syllables that were dominant or preferred in their repertoire. A few syllables were dominant or preferred for more than one individual; the syllables 1A, 1FF, 1ZZ, and 3B were among the dominant syllables of two or more individuals. However, the relative importance of these syllables varied from individual to individual, and most of the dominant syllables were dominant for only one individual. This reflects the results of the network analysis and other comparisons of repertoire content and structure: some individuals share syllables to a certain extent, but their proportional use of those syllables varies considerably from individual to individual. As with previous results, these results could have been artificially affected by varying lengths or temporal distribution of observation time for each individual. More observational data for each individual, or observations from a different time or behavioral context, could also provide different results.

General confounding factors

Because of the long distances ‘i‘iwi are known to travel, I considered ‘i‘iwi at the Pua‘Ākala and Pedro banding sites to be part of the same population. However, territorial singing is likely to be strictly a breeding season behavior, so song-matching may occur locally among ‘i‘iwi at Pua‘Ākala and Pedro with differences between sites. A number of syllable types were observed at both sites, so it is clear that there is some meme flow between Pua‘Ākala and Pedro. However, it is possible that the repertoires of ‘i‘iwi at the two sites are not truly comparable. Additionally, in my primary data collection season of spring 2015, I visited Pedro later in the season (May 15 to June 13, 2015) than Pua‘Ākala (February 21 to May 4, 2015). ‘I‘iwi recorded at Pedro may have been, on average, at a different stage in the breeding cycle than
‘i’iwi recorded at Pua ‘Ākala, and therefore may have exhibited behavioral differences. The geographic and temporal differences between the ‘i’iwi observed at the two sites may have artificially inflated the amount of individual variability observed, reducing statistical power and potentially masking the effects of sex on vocal behavior.

Although an accumulation curve test indicated that I had observed each individual long enough to capture most of their repertoire, it is certain that I did not capture the entirety of every individual’s repertoire. Even the supposition that I succeeded in capturing most of each individual’s repertoire depends on the assumption that ‘i’iwi do not change their set of vocalized syllable types over time. ‘I’iwi may have a “hidden repertoire” of syllables that they have heard or memorized but have not vocalized for a long period of time (Chaiken et al. 1994). Some syllables in an ‘i’iwi’s active repertoire may merely be sung very infrequently, avoiding my detection (Garamszegi et al. 2005); this is supported by the variability in frequency of use of various syllables in each ‘i’iwi’s observed repertoire. These factors may have artificially affected the observed size and content of ‘i’iwi repertoires in this study.

Finally, my recorded observations of ‘i’iwi repertoires may not reflect the behavior of the birds with complete accuracy and precision. The data set may contain false negatives, i.e., when a target ‘i’iwi vocalized but I did not identify and include the vocalization in the data set. This could occur if I made insufficient verbal notes in the field, or if the ‘i’iwi vocalized very quietly, among other reasons. The data set may also contain false positives, i.e., when a non-target ‘i’iwi vocalized and I mistakenly attributed that vocalization to my target bird. This could occur if I made insufficient verbal notes in the field, if there were other ‘i’iwi in the close vicinity, or if I had an insufficiently clear view of my target bird, among other reasons. Both false negatives and
false positives could have artificially affected the resulting observed repertoire size, repertoire content, and vocalization rate for all individuals.

Conclusion

Overall, this study reveals previously unknown details about ‘i‘iwi vocal behavior. Both males and females engage in duetting and solo singing. Female ‘i‘iwi occasionally vocalize, even sing, from the nest. ‘I‘iwi vocal behavior is characterized by high individual variability, much more so than the variability between sexes. For ‘i‘iwi, the unit of cultural transmission, or meme, is the syllable, and there is a large pool of syllables within a given population, from which pool each individual learns a comparatively small selection.

This study is a first step in the process of understanding the complexities of ‘i‘iwi vocal behavior. The differences in vocal behavior, or lack thereof, between male and female ‘i‘iwi shed light on the divergence or convergence of sex roles in this species. Understanding ‘i‘iwi individual repertoire size and content, the degree of similarity between the repertoires of neighboring ‘i‘iwi, and the high degree of individuality will help future researchers understand the challenges involved in using acoustic data to estimate the size and demographic makeup of ‘i‘iwi populations.

On a broader scale, this study is significant in providing a baseline of knowledge about ‘i‘iwi vocal behavior. Acquiring this information adds to the pool of data researchers can use to study the complexities of songbird evolution worldwide, i.e., what factors of evolutionary history or natural history characteristics drive song variability across the oscine clade, and why? As a tropical, monomorphic species with female solo singing and duetting, and as a species that does not migrate but also does not maintain a year-round territory, the ‘i‘iwi is a member of a number
of understudied groups, and can therefore contribute greatly to our understanding of songbird diversity.

This study is significant particularly in regards to documenting the vocal behavior of female ‘i’iwi. Odom and Benedict (2018) have made a solid argument for better documentation of female singing across the songbird clade, and especially in the tropics. Female song is disproportionately underrepresented in the literature and in biological collections despite being widespread, even among temperate species (Webb et al. 2016). Detailed descriptions of female song structure and output are rare. Accurate documentation of both male and female singing is particularly scarce among monochromatic, tropical species, due to a historic lack of resources directed toward tropical species and the difficulty of identifying sex in the field. Having more accurate and detailed information on female singing can provide insights into songbird neurobiology, physiology, behavioral ecology, evolutionary biology, and conservation biology.

The results of this study lead to a number of potential future research questions. It would be interesting to pursue whether ‘i’iwi exhibit song sharing with their neighbors. Ralph and Fancy (1995) found that ‘i’iwi have high site fidelity over a period of several years, which suggests that ‘i’iwi have the same neighbors long-term. Song sharing would be advantageous under these circumstances. Future researchers should compare ‘i’iwi from different populations in order to determine to what degree they have syllables in common, and whether neighboring ‘i’iwi share more syllables than distant ‘i’iwi. Experimental studies could examine how ‘i’iwi react to syllables from outside their population compared to syllables from inside their population.

Along a related line, the question remains unanswered whether ‘i’iwi are open-ended learners, i.e., do their repertoires change over time? If song sharing is an important feature of
their behavior, it would be advantageous for them to maximize their finite capacity for memes in their repertoire by swapping out for more relevant memes as their network of neighbors changes over time. Observing the vocal behavior of the same individuals over multiple years would help researchers to determine whether ‘i‘iwi add and drop syllables over time.

In the accumulation curve of new syllables added as new individuals were added to the pool (used in assessing statistical power in this study), the slope of the curve was steep and showed no sign of flattening. The size of the syllable pool within a population of ‘i‘iwi is therefore currently unknowable, but presumably very large. It would be worth investigating the size of a population’s syllable pool, how many individual repertoires would be needed in order to capture most of that syllable pool, and why the syllable pool is so large. Do ‘i‘iwi improvise memes based on memes they have heard, or even invent entirely new memes, as some songbird species are known to do (Beecher and Brenowitz 2005)? This would help to explain the high diversity of syllables and the high proportion of syllables that seem to be unique to a single individual’s repertoire.

In this study, I chose to record during ‘i‘iwi peak breeding season because of increased singing in general during that time of year. However, during breeding season, a large proportion of female ‘i‘iwi are nest-sitting, and with one big exception in my study group, most females tend to be quiet while on the nest. All aspects of vocal behavior including comparisons between male and female vocal behavior may be different during a different season. A lot could be learned about ‘i‘iwi behavior in general and sex differences in ‘i‘iwi behavior specifically by studying ‘i‘iwi vocalizations in other times of the year, when they are not defending a breeding territory.
Finally, a comparison of the high diversity of ‘i‘iwi memes with that of other Hawaiian oscines—such as the meme-diverse ‘apapane and ‘ōma‘o or the relatively meme-poor Hawai‘i ‘amakihi and Hawai‘i ‘elepaio—in the context of evolutionary history or various natural history characteristics could clarify ways in which these factors correlate with the evolution of different vocal behaviors in Hawaiian oscine species.
Literature Cited


Cicero, C., and M. Benowitz-Fredericks. 2000. Song types and variation in insular populations of Lincoln’s Sparrow (Melospiza lincolnii), and comparisons with other Melospiza. The Auk 117: 52-64.


Appendix

a)
Figure 11, a.-o. Spectrograms of the 182 unique ‘i’iwi syllable types observed to be used by study individuals. Where more than one syllable is pictured in the spectrogram, the featured syllable type is indicated by a red selection box.